

## Degrees of Sexual Dimorphism in *Cebus* and Other New World Monkeys

THOMAS J. MASTERSON<sup>1</sup>\* AND WALTER CARL HARTWIG<sup>2</sup>

<sup>1</sup>Department of Biology, James Madison University, Harrisonburg, Virginia 22807

<sup>2</sup>Department of Basic Sciences, Touro University College of Osteopathic Medicine, San Francisco, California 94115

**KEY WORDS** body size; capuchin; platyrrhines; Greene's *t*-test; canines

**ABSTRACT** Sexual dimorphism in primate species expresses the effects of phylogeny, life history, behavior, and ontogeny. The causes and implications of sexual dimorphism have been studied in several different primates using a variety of morphological databases such as body weight, canine length, and coat color and ornamentation. In addition to these different patterns of dimorphism, the degree to which a species is dimorphic results from a variety of possible causes. In this study we test the general hypothesis that a species highly dimorphic for one size-based index of dimorphism will be equally dimorphic (relative to other species) for other size-based indices. Specifically, the degree and pattern of sexual dimorphism in *Cebus* and several other New World monkey species is measured using craniometric data as a substitute for the troublesome range of variation in body weight estimates. In general, the rank ordering of species for dimorphism ratios differs considerably across neural vs. non-neural functional domains of the cranium. The relative degree of sexual dimorphism in different functional regions of the cranium is affected by the independent action of natural selection on those regions. Regions of the cranium upon which natural selection is presumed to have acted within a species show greater degrees of dimorphism than do the same regions in closely related taxa. Within *Cebus*, *C. apella* is consistently more dimorphic than other *Cebus* species for facial measurements, but not for neural or body weight measurements. The pattern in *C. apella* indicates no single best measurement of the degree of dimorphism in a species; rather, the relative degree of dimorphism applies only to the region being measured and may be enhanced by other selective pressures on morphology. *Am J Phys Anthropol* 107:243-256, 1998. © 1998 Wiley-Liss, Inc.

Sexual dimorphism can be expressed through body size, canine size, and coat color and/or ornamentation. Different selective pressures presumably underlie these different patterns of dimorphism, and several theoretical models for the evolution of canine and body size dimorphism in primates have been proposed (Clutton-Brock et al., 1977; Leutenegger and Kelly, 1977; Oxnard, 1983; Clutton-Brock, 1985; Pickford, 1986; Leigh, 1992, 1995; Martin et al., 1994). The

degree of sexual dimorphism in a species may be a function of its overall body size and/or phylogenetic inertia (Leutenegger and Cheverud, 1982, 1985). The pattern of dimorphism, however, is usually attributed to

Grant sponsor: Sigma XI; Grant sponsor: University of California Regents.

\*Correspondence to: Dr. Thomas J. Masterson, Department of Biology, James Madison University, Harrisonburg, VA 22807. E-mail: mastertj@jmu.edu

Received 20 December 1996; accepted 30 July 1998.

some form of intraspecific competition (Plavcan and van Schaik, 1992, 1994, 1997). Studies comparing data *across* primate radiations concluded that overall body size most directly determines the degree of dimorphism (Leutenegger, 1978; Leutenegger and Cheverud, 1982, 1985; Cheverud et al., 1985). Studies *within* primate radiations, however, dismiss body size as an important factor in the degree or pattern of dimorphism within those radiations (Gaulin and Sailer, 1984; Kappeler, 1990, 1991; Ford, 1994). The relationship between degree and pattern of dimorphism in the same species has not been explored as closely.

New World monkeys present a useful group for examining hypotheses of sexual dimorphism. The radiation includes some well-defined monophyletic clades within which phylogeny can be controlled. New World monkeys range from roughly 100 g to 10 kg, and thus are a useful radiation for examining the effects of body size. Several studies have investigated the degree and pattern of canine sexual dimorphism in New World monkeys (Kay et al., 1988; Plavcan and Kay, 1988; Greenfield, 1992) or incorporated data for New World monkeys in larger studies of dimorphism in anthropoids (Leutenegger, 1978; Leutenegger and Cheverud, 1982, 1985; Cheverud et al., 1985; Oxnard et al., 1985; Leigh 1992, 1995; Plavcan and van Schaik, 1992, 1994, 1997). In this study we evaluate the craniometric expression of dimorphism in New World monkeys in order to test hypotheses of how general characters (body size, competition) affect specific anatomies (neurocranium, face, dental arcade). We are interested in the particular question of whether sexual dimorphism in different functional regions of the cranium is affected by the independent action of natural selection on those regions.

Ford (1994) recently evaluated body weight dimorphism in New World monkeys. To the extent that the subfamilies Pitheciinae (*Pithecia*, *Chiropotes*, *Cacajao*), Callitrichinae (*Callithrix*, *Cebuella*, *Saguinus*, *Leontopithecus*, *Callimico*) and Atelinae (*Ateles*, *Brachyteles*, *Lagothrix*, *Alouatta*) represent monophyletic clades, relative body size and

phylogeny do not correlate well to the degree of body weight dimorphism evident in platyrrhines. Ford (1994) cautioned, however, that estimates of mean body weight range widely from one study to another, and that accurate data for many species are lacking. A comparison of some of the most important references for platyrrhine body weight (Harvey et al., 1987; Ford and Davis, 1992; Leigh, 1994; Plavcan and van Schaik, 1997) confirms the troublesome situation identified by several recent studies (Hartwig, 1996; Plavcan and van Schaik, 1997; Smith and Jungers, 1997). The present study follows from Ford's (1994) suggestion that sexual dimorphism in New World monkeys should be evaluated on a database comparable to body weight but internally more accurate and complete with summary statistics. We attempt to do this using a database of New World monkey cranial measurements and Greene's (1989) *t*-test for measuring the degree of difference between two dimorphic populations.

In this study we evaluate the following hypotheses: 1) the absolute and relative degrees of sexual dimorphism across taxa vary (within the same dimensional measurement) according to the function of the structure whose size is measured; and 2) as a function of phylogenetic inertia, closely related dimorphic species will express similar degrees of dimorphism within the same functional region of the cranium. The first hypothesis predicts that the cranium, as a composite of neural and somatic growth factors, will not be uniformly dimorphic in a species that otherwise displays strong body weight dimorphism or canine size dimorphism; thus, a rank ordering of species for body weight dimorphism or canine size dimorphism will not equal rank orderings of species for morphometric dimorphism in separate functional regions of the cranium. The second hypothesis predicts that the effects of natural selection on specific parts of the cranium will not affect the degree to which closely related species express craniometric sexual dimorphism. This prediction can be applied to the genus *Cebus*, in which one species (*C. apella*) occupies a slightly different ecological niche than the other three species (Janson and Boinski, 1992) and presents slightly more robust mastication.

TABLE 1. Sample sizes and taxonomic distribution for cranial morphometric data

Species	Male	Female	Total
<i>Alouatta palliata</i>	18	20	38
<i>Aotus nancymai</i>	23	37	60
<i>Ateles paniscus</i>	16	9	25
<i>Cacajao calvus</i>	16	12	28
<i>Callicebus cupreus</i>	26	22	48
<i>Cebus albifrons</i>	43	43	86
<i>Cebus apella</i>	67	50	117
<i>Cebus capucinus</i>	42	42	84
<i>Cebus olivaceus</i>	40	38	78
<i>Lagothrix lagotricha</i>	40	33	73
<i>Pithecia pithecia</i>	27	9	36
<i>Saguinus fuscicollis</i>	25	18	43
<i>Saimiri sciureus</i>	70	47	117
Total	453	380	833

tory anatomy (Kinzey, 1974). This intragenetic comparison offers an opportunity to examine dimorphism while keeping the effects of phylogeny and body size as controlled as possible.

#### MATERIALS AND METHODS

Body weight, canine size, and cranial size data were collected for most New World monkey genera except the monomorphic marmosets and tamarins. Sample sizes for the cranial data are presented in Table 1. Cranial morphometric data were collected on over 800 adult individuals using digital calipers or a Reflex microscope (see Table 2 for measurements). Raw data and summary statistics for these measurements can be found in Hartwig (1993) and Masterson (1996). Body weight data from several recent studies are presented to illustrate the variation present in this database (Ford and Davis, 1992, Leigh, 1994, Plavcan and van Schaik, 1997; Smith and Jungers, 1997).

Because the data analyzed below were collected in different studies on different species of New World monkey genera, our list of species for cranial dimorphism data does not overlap completely with the results for body weight and canine size dimorphism (with the exception of *Cebus*). Interspecific differences in sexual dimorphism within the same genus of New World monkey, however, are not apparent from the few studies that have examined platyrrhines in detail (Hartwig, 1993; Ford 1994), again with the exception of *Cebus* (Masterson, 1996). In general, then, we believe that the results

reported below represent the degree and pattern of sexual dimorphism expressed in the genera of New World monkeys analyzed below.

Interspecific dimorphism is examined using a simple ratio of male mean / female mean for body weight, canine size, and craniometric data. Our hypotheses predict that dimorphism is a condition of mosaic expression that should not be expressed uniformly across a morphometric domain such as the skull. Taxonomic rank orders of dimorphism ratios, therefore, should not be consistent across the cranial measurements taken for this study. A Spearman rank-order correlation test was performed on comparisons of the measurements in order to identify which measurements produce significantly similar taxonomic rank orders.

We are aware that simple ratios do not control for size differences, except under special circumstances which are not met by our data (Albrecht et al., 1993). Various size-adjustment techniques reviewed by Albrecht et al. (1993) all introduce size-related changes in the distributional characteristics (variances) that differentially alter relationships among animals that belong to different size classes; therefore, we continue to use the simple ratio as a statistic of dimorphism. In addition, we are not interested in examining size and shape separately in the contents of this study; therefore, we do not use Mosimann's family of shape ratios as suggested by Jungers et al. (1995).

Interspecific differences in the degree of dimorphism were examined using Greene's (1989) *t*-test for 15 cranial measurements (Table 2). Greene's *t*-test is mathematically equivalent to the Relethford and Hodges (1985) test, but easier to apply. Only summary statistics are needed to perform this test, and it yields a robust index of how much more dimorphic one population is compared to another (Konigsberg, 1991). In this study we use Greene's *t*-test as a multiple comparison test to examine differences in degree of dimorphism between two populations. The significance level is the probability of finding at least one type I error, i.e., the probability of falsely rejecting at least one

TABLE 2. Cranial measurements

Abbreviation	Domain	Measurement	Definition
BOB	Neural	Biorbital breadth	Maximum distance between lateral orbital margins
BMB	Facial	Bimaxillary breadth	Right zygomaxillare inferior to left zygomaxillare inferior
PAL	Facial	Palate length	Maximum length of the hard palate at midline
BCB	Facial	Bicanine breadth	Maximum distance across the outer alveoli of the canines
PAB	Facial	Palate breadth	Maximum distance across palate posterior to canines
FH	Facial	Facial height	Nasion to infradentale superior
BZB	Facial	Bizygomatic breadth	Maximum distance between the zygomatic arches
MCL	Neural	Max. cranial length	Lambda to infradentale superior
NCL	Neural	Neurocranial length	Lambda to glabella
NCB	Neural	Neurocranial breadth	Maximum breadth across parietals
NCH	Neural	Neurocranial height	Vertex to basion
BMW	Neural	Bimastoid width	Maximum breadth across mastoid processes
POC	Neural	Postorbital breadth	Minimum breadth between the speno-parietal sutures
B-N	Neural	Basicranial length	Basion to nasion
B-P	Neural	Basicranial flexion	Basion to prosthion

TABLE 3. Indices of body weight and canine size dimorphism in New World Monkeys (subfamily taxonomy following Schneider and Rosenberger, 1996)

Taxon	Body weight dimorphism (Leigh, 1994)		Body weight dimorphism (wild) (Ford and Davis, 1992)	Body weight dimorphism (wild) (Smith and Jungers, 1997)	Body weight dimorphism (wild) (Plavcan and van Schaik, 1997)	Canine height dimorphism (Plavcan and Kay, 1988)	Canine diameter dimorphism (Kay et al., 1988)
	Wild	Captive					
Atelinae							
<i>Alouatta caraya</i>	1.41	1.85	1.48	1.48	1.53	1.48	1.34
<i>Alouatta palliata</i>			1.34	1.34	1.28	1.51	1.28
<i>Alouatta fusca</i>			1.36	1.55	1.37	1.52	1.40
<i>Alouatta belzebul</i>			1.32	1.32	1.39	1.81	1.42
<i>Alouatta seniculus</i>			1.28	1.28	1.26	1.50	1.31
<i>Ateles geoffroyi</i>	1.20	1.34	1.10	1.07	1.25	1.52	1.11
<i>Ateles paniscus</i>			0.85	1.08	1.10	1.57	1.10
<i>Lagothrix lagotricha</i>	1.35		1.45	1.04	1.20	1.88	1.22
Pitheciinae							
<i>Cacajao calvus</i>			1.20	1.20	1.20		
<i>Pithecia pithecia</i>	1.27		1.14	1.23	1.19	1.32	1.18
<i>Aotus nancymai</i>			0.98	1.02			
<i>Aotus trivirgatus</i>	1.07	0.98	0.97	1.10	0.99	1.08	1.04
<i>Callicebus cupreus</i>			0.90	0.91			
<i>Callicebus moloch</i>	1.03	1.08	1.16	1.07	1.09	1.08	0.99
Cebinae							
<i>Cebus albifrons</i>	1.22		1.37	1.39			
<i>Cebus apella</i>	1.42	1.91	1.28	1.45	1.38	1.41	1.22
<i>Cebus capucinus</i>			1.45	1.45			1.16
<i>Cebus olivaceus</i>			1.24	1.30	1.40		
<i>Saimiri sciureus</i>	1.25	1.47	1.26	1.18	1.22	1.61	1.17
Callitrichinae							
<i>Saguinus fuscicollis</i>	1.19	0.98	0.96	0.96	1.00	1.03	0.98

null hypothesis during the course of comparing all means. It is referred to as an experimentwise error rate rather than a comparisonwise error rate (Zar, 1984). The significance level was determined using a Bonferroni adjustment, dividing the single-comparison level ( $\alpha = 0.05$ ) by the number of possible comparisons, i.e.,  $\alpha' = \alpha / k$ . This provides a conservative approach in which one lowers the type I error of significance for each comparison so that the probability of making any type I error at all in the entire

series of tests does not exceed  $\alpha$  (Sokal and Rohlf, 1995).

## RESULTS

Table 3 reports body weight and canine size dimorphism ratios from the literature (Kay et al., 1988; Plavcan and Kay, 1988; Ford, 1994; Leigh, 1994; Plavcan and van Schaik, 1997; Smith and Jungers, 1997). Indices of body weight dimorphism and thus the rank ordering depend on what mean weights are considered most accurate. This

is not a trivial matter, as demonstrated recently by Smith (1996) for *Ateles paniscus*. The studies considered here (Ford, 1994; Leigh, 1994; Plavcan and van Schaik, 1997) indicate that *Alouatta*, *Cebus*, and *Lagothrix* are significantly sexually dimorphic for body weight. Some taxa, such as *Alouatta*, are dimorphic for both body weight and canine measures; however, some taxa, such as *Ateles*, *Pithecia*, and *Saimiri*, are more dimorphic for one measure than for the other. Plavcan and van Schaik (1997) concluded that a strong association between male-male competition and body weight dimorphism in anthropoid primates indicated that sexual selection was a major factor in the evolution of body weight dimorphism.

Canine dimorphism has been measured as height dimorphism (Plavcan and Kay, 1988) and breadth dimorphism (Kay et al., 1988). In both cases, taxa that are scored to have high degrees of male-male competition (Ford, 1994; Plavcan and van Schaik, 1997), such as *Alouatta* and *Cebus apella*, rank as highly dimorphic for canine size. The opposite, however, is not also true. Taxa such as *Saimiri*, *Lagothrix*, and *Ateles paniscus*, which are scored to have intermediate degrees of male-male competition (Ford, 1994; Plavcan and van Schaik, 1997), also rank highly for canine height dimorphism. No other niche parameter scored by Ford (1994) unites these taxa to the exclusion of others. In other words, all New World monkeys that exhibit strong male-male competition (according to Ford, 1994) display sexually dimorphic canines, but the feature of canine sexual dimorphism is not the result of a minimum degree of male-male competition.

Estimates of sexual dimorphism for neural and facial cranial measurements are reported as indices (Table 4) and as Greene's (1989) *t*-test (Tg) values (Tables 5–11). *Cebus* and *Alouatta* are the most consistently dimorphic taxa for cranial size measurements in our study, which is consistent with their rankings for body weight dimorphism. Which of these genera shows a greater degree of dimorphism depends to some extent on whether the measurement is neurocranial and on whether the measurement concerns a region of the skull subject to other selection pressures. With this in mind, *C.*

*apella* is slightly more dimorphic for most of the neurocranial measurements (biorbital breadth, neurocranial length, biamastoid breadth), whereas *A. palliata* is slightly more dimorphic for most of the palatal and lower face measurements (palate breadth, palate length, bicanine breadth, bimaxillary width). Regardless of which taxa is more dimorphic, the degree of dimorphism is lower for neurocranial measurements than for facial measurements.

The two genera that display strong canine but not body size dimorphism display different patterns of cranial dimorphism. *Saimiri* displays moderate body weight dimorphism, strong canine size dimorphism, and moderate cranial dimorphism. *Ateles paniscus* appears to be as monomorphic for cranial size as Smith (1996) suggests it is for body weight dimorphism, and thus distinctly less dimorphic than it scores for canine size. These results suggest that the cranial measures used in this study generally reflect trends in body size dimorphism, as suggested by Ford (1994). They also demonstrate that rank orders of dimorphism are not taxonomically consistent for different aspects of the cranium.

The difference in degree of dimorphism between taxa was evaluated using Greene's (1989) *t*-test. Results are reported as comparisons between 1) the "most" cranially dimorphic taxon, *A. palliata* and the other taxa (Tables 5, 6), 2) the variously dimorphic capuchin species and other genera (Tables 7–10), and 3) the different species of *Cebus* (Table 11). Measurements for which no genus is significantly more dimorphic than another are biamastoid breadth and cranial vault height. Measurements for which *Alouatta* is significantly more dimorphic than all other New World monkeys are basicranial length and basicranial flexion (basion-prosthion).

Because this study predicts that taxonomic rank orders for degree of dimorphism as measured by cranial variables will differ from that measured by body weight, a Spearman rank-order correlation test was performed (Table 12). Correlation coefficient values are also presented for taxonomic rank orders of the degree of dimorphism as measured by facial and neural variables



TABLE 4. Indices of sexual dimorphism for selected cranial measurements

Species	BOB	Species	BMW	Species	PAL	Species	BCB
<i>C. apella</i>	1.07	<i>A. palliata</i>	1.17	<i>A. palliata</i>	1.14	<i>A. palliata</i>	1.20
<i>C. albifrons</i>	1.06	<i>C. apella</i>	1.15	<i>C. apella</i>	1.11	<i>C. apella</i>	1.16
<i>C. olivaceus</i>	1.06	<i>C. albifrons</i>	1.12	<i>C. capucinus</i>	1.09	<i>C. capucinus</i>	1.16
<i>C. capucinus</i>	1.05	<i>L. lagotricha</i>	1.09	<i>L. lagotricha</i>	1.09	<i>S. sciureus</i>	1.15
<i>A. palliata</i>	1.05	<i>C. olivaceus</i>	1.08	<i>C. albifrons</i>	1.08	<i>C. albifrons</i>	1.12
<i>C. calvus</i>	1.04	<i>C. capucinus</i>	1.08	<i>C. olivaceus</i>	1.07	<i>C. olivaceus</i>	1.12
<i>S. sciureus</i>	1.03	<i>C. calvus</i>	1.08	<i>S. sciureus</i>	1.07	<i>L. lagotricha</i>	1.12
<i>C. cupreus</i>	1.02	<i>S. sciureus</i>	1.08	<i>C. calvus</i>	1.03	<i>C. calvus</i>	1.07
<i>L. lagotricha</i>	1.02	<i>A. paniscus</i>	1.04	<i>A. nancymai</i>	1.02	<i>A. paniscus</i>	1.04
<i>A. nancymai</i>	1.01	<i>C. cupreus</i>	1.02	<i>P. pithecia</i>	1.01	<i>P. pithecia</i>	1.02
<i>P. pithecia</i>	1.00	<i>S. fuscicollis</i>	1.02	<i>A. paniscus</i>	1.01	<i>S. fuscicollis</i>	1.01
<i>S. fuscicollis</i>	1.00	<i>P. pithecia</i>	1.01	<i>S. fuscicollis</i>	0.99	<i>A. nancymai</i>	1.00
<i>A. paniscus</i>	0.98	<i>A. nancymai</i>	1.00	<i>C. cupreus</i>	0.98	<i>C. cupreus</i>	0.99
Species	PAB	Species	BZB	Species	NCL	Species	NCB
<i>A. palliata</i>	1.09	<i>C. apella</i>	1.17	<i>C. apella</i>	1.06	<i>A. palliata</i>	1.05
<i>C. apella</i>	1.07	<i>A. palliata</i>	1.15	<i>C. albifrons</i>	1.05	<i>C. albifrons</i>	1.03
<i>C. capucinus</i>	1.07	<i>C. albifrons</i>	1.12	<i>A. palliata</i>	1.04	<i>C. apella</i>	1.03
<i>C. albifrons</i>	1.06	<i>C. capucinus</i>	1.12	<i>C. capucinus</i>	1.04	<i>C. capucinus</i>	1.02
<i>C. olivaceus</i>	1.05	<i>C. olivaceus</i>	1.10	<i>C. olivaceus</i>	1.04	<i>C. olivaceus</i>	1.02
<i>C. calvus</i>	1.01	<i>S. sciureus</i>	1.10	<i>C. calvus</i>	1.03	<i>A. paniscus</i>	1.01
<i>L. lagotricha</i>	1.01	<i>C. calvus</i>	1.08	<i>L. lagotricha</i>	1.02	<i>C. calvus</i>	1.01
<i>A. nancymai</i>	1.00	<i>L. lagotricha</i>	1.08	<i>A. nancymai</i>	1.01	<i>C. cupreus</i>	1.01
<i>C. cupreus</i>	1.00	<i>A. paniscus</i>	1.04	<i>A. paniscus</i>	1.01	<i>A. nancymai</i>	1.00
<i>P. pithecia</i>	1.00	<i>C. cupreus</i>	1.01	<i>S. sciureus</i>	1.01	<i>L. lagotricha</i>	1.00
<i>S. sciureus</i>	0.99	<i>P. pithecia</i>	1.01	<i>C. cupreus</i>	1.00	<i>S. sciureus</i>	1.00
<i>A. paniscus</i>	0.98	<i>A. nancymai</i>	1.00	<i>P. pithecia</i>	1.00	<i>P. pithecia</i>	0.99
<i>S. fuscicollis</i>	0.98	<i>S. fuscicollis</i>	0.99	<i>S. fuscicollis</i>	0.98	<i>S. fuscicollis</i>	0.99
Species	NCH	Species	FH	Species	MCL	Species	POC
<i>C. apella</i>	1.07	<i>C. apella</i>	1.13	<i>A. palliata</i>	1.09	<i>C. apella</i>	1.04
<i>A. palliata</i>	1.04	<i>A. palliata</i>	1.12	<i>C. apella</i>	1.08	<i>A. palliata</i>	1.03
<i>C. albifrons</i>	1.04	<i>C. albifrons</i>	1.10	<i>C. albifrons</i>	1.07	<i>C. calvus</i>	1.03
<i>C. calvus</i>	1.03	<i>C. capucinus</i>	1.10	<i>C. capucinus</i>	1.06	<i>A. paniscus</i>	1.02
<i>C. capucinus</i>	1.02	<i>C. olivaceus</i>	1.08	<i>C. olivaceus</i>	1.06	<i>C. albifrons</i>	1.02
<i>C. olivaceus</i>	1.02	<i>C. cupreus</i>	1.05	<i>L. lagotricha</i>	1.05	<i>C. olivaceus</i>	1.02
<i>S. sciureus</i>	1.02	<i>L. lagotricha</i>	1.05	<i>S. sciureus</i>	1.04	<i>S. sciureus</i>	1.02
<i>C. cupreus</i>	1.01	<i>S. sciureus</i>	1.05	<i>C. calvus</i>	1.03	<i>L. lagotricha</i>	1.01
<i>S. fuscicollis</i>	1.01	<i>C. calvus</i>	1.01	<i>A. nancymai</i>	1.01	<i>C. cupreus</i>	1.00
<i>A. nancymai</i>	1.00	<i>A. nancymai</i>	1.00	<i>A. paniscus</i>	1.00	<i>C. capucinus</i>	1.00
<i>A. paniscus</i>	1.00	<i>A. paniscus</i>	1.00	<i>C. cupreus</i>	1.00	<i>A. nancymai</i>	0.98
<i>L. lagotricha</i>	0.99	<i>S. fuscicollis</i>	1.00	<i>P. pithecia</i>	1.00	<i>P. pithecia</i>	0.97
<i>P. pithecia</i>	0.99	<i>P. pithecia</i>	0.98	<i>S. fuscicollis</i>	0.99	<i>S. fuscicollis</i>	0.97
Species	BMW	Species	B-N	Species	B-P	Overall	Avg.
<i>C. apella</i>	1.08	<i>A. palliata</i>	1.15	<i>A. palliata</i>	1.15	<i>A. palliata</i>	1.106
<i>C. albifrons</i>	1.07	<i>C. apella</i>	1.11	<i>C. apella</i>	1.13	<i>C. apella</i>	1.097
<i>C. capucinus</i>	1.06	<i>C. albifrons</i>	1.09	<i>C. albifrons</i>	1.11	<i>C. albifrons</i>	1.076
<i>C. olivaceus</i>	1.05	<i>C. capucinus</i>	1.09	<i>C. capucinus</i>	1.11	<i>C. capucinus</i>	1.071
<i>A. palliata</i>	1.04	<i>C. olivaceus</i>	1.08	<i>C. olivaceus</i>	1.09	<i>C. olivaceus</i>	1.063
<i>C. calvus</i>	1.03	<i>C. calvus</i>	1.06	<i>S. sciureus</i>	1.07	<i>S. sciureus</i>	1.045
<i>L. lagotricha</i>	1.03	<i>S. sciureus</i>	1.05	<i>C. calvus</i>	1.06	<i>L. lagotricha</i>	1.044
<i>A. paniscus</i>	1.02	<i>L. lagotricha</i>	1.04	<i>L. lagotricha</i>	1.06	<i>C. calvus</i>	1.040
<i>S. fuscicollis</i>	1.01	<i>A. nancymai</i>	1.02	<i>A. nancymai</i>	1.02	<i>A. paniscus</i>	1.011
<i>S. sciureus</i>	1.00	<i>A. paniscus</i>	1.02	<i>P. pithecia</i>	1.01	<i>C. cupreus</i>	1.007
<i>C. cupreus</i>	0.99	<i>C. cupreus</i>	1.01	<i>A. paniscus</i>	1.00	<i>A. nancymai</i>	1.003
<i>P. pithecia</i>	0.99	<i>P. pithecia</i>	1.01	<i>C. cupreus</i>	1.00	<i>P. pithecia</i>	0.999
<i>A. nancymai</i>	0.98	<i>S. fuscicollis</i>	1.01	<i>S. fuscicollis</i>	1.00	<i>S. fuscicollis</i>	0.997

compared to one another. The results of the Spearman test indicate that the taxonomic rank order for degree of dimorphism as measured by body weight differs from the taxonomic rank orders derived from all five

facial and all five neural measurements. Within the craniometric database, 14 of a possible 55 comparisons show statistically similar taxonomic rank orders. Of these 14, four are between two facial variables and

TABLE 5. *Tg* values for *A. palliata* vs. other New World monkeys

Variables	<i>A. palliata</i> vs. <i>A. nancymai</i>	<i>A. palliata</i> vs. <i>A. paniscus</i>	<i>A. palliata</i> vs. <i>C. calvus</i>	<i>A. palliata</i> vs. <i>C. cupreus</i>	<i>A. palliata</i> vs. <i>L. lag.</i>	<i>A. palliata</i> vs. <i>P. pithecia</i>	<i>A. palliata</i> vs. <i>S. fuscicollis</i>	<i>A. palliata</i> vs. <i>S. sciureus</i>
Biorbital width	2.55	<b>2.86</b>	0.86	2.26	1.51	2.41	<b>3.08</b>	<b>2.88</b>
Bimaxillary width	<b>5.73</b>	2.51	1.46	<b>4.45</b>	0.09	<b>3.74</b>	<b>4.49</b>	<b>3.57</b>
Palate length	<b>6.52</b>	<b>4.91</b>	<b>3.81</b>	<b>6.85</b>	<b>2.73</b>	<b>4.68</b>	<b>6.91</b>	<b>7.27</b>
Bicanine breadth	<b>10.55</b>	<b>6.61</b>	<b>3.81</b>	<b>10.29</b>	<b>2.63</b>	<b>5.42</b>	<b>10.47</b>	<b>5.29</b>
Palate breadth	<b>6.71</b>	<b>4.64</b>	<b>4.24</b>	<b>6.26</b>	<b>5.99</b>	<b>4.25</b>	<b>5.77</b>	<b>9.48</b>
Facial height	<b>5.11</b>	<b>3.84</b>	<b>3.24</b>	<b>3.72</b>	<b>2.94</b>	<b>3.84</b>	<b>5.05</b>	<b>5.13</b>
Bizygomatic breadth	<b>11.05</b>	<b>6.15</b>	<b>4.14</b>	<b>9.54</b>	<b>5.59</b>	<b>6.74</b>	<b>9.51</b>	<b>9.06</b>
Neurocranial length	1.93	1.44	0.61	2.32	1.00	1.79	<b>2.97</b>	2.54
Neurocranial breadth	<b>4.78</b>	<b>2.70</b>	2.30	<b>4.02</b>	<b>3.82</b>	<b>3.60</b>	<b>5.27</b>	<b>4.94</b>
Maximum cranial length	<b>6.36</b>	<b>5.23</b>	<b>3.02</b>	<b>6.51</b>	<b>2.82</b>	<b>4.30</b>	<b>6.70</b>	<b>6.08</b>
Bimastoid width	1.98	0.33	0.28	1.68	0.06	1.45	1.30	2.13
Postorbital constriction	<b>4.10</b>	-0.05	0.23	2.44	1.56	<b>4.05</b>	<b>4.18</b>	2.06
Basicranial length	<b>7.93</b>	<b>5.56</b>	<b>4.40</b>	<b>9.43</b>	<b>6.29</b>	<b>6.18</b>	<b>9.76</b>	<b>9.59</b>
Basicranial flexion	<b>9.09</b>	<b>7.42</b>	<b>4.18</b>	<b>9.18</b>	<b>4.61</b>	<b>5.71</b>	<b>9.61</b>	<b>9.22</b>
Neurocranial height	1.75	0.75	0.23	1.57	2.06	2.29	2.08	1.32

**Bold** = significant difference in degree of dimorphism at  $P \leq 0.006$ .

TABLE 6. *Tg* values for *A. palliata* vs. *Cebus* species

Variables	<i>A. palliata</i> vs. <i>C. albifrons</i>	<i>A. palliata</i> vs. <i>C. apella</i>	<i>A. palliata</i> vs. <i>C. capucinus</i>	<i>A. palliata</i> vs. <i>C. olivaceus</i>
Biorbital width	0.23	-0.20	0.76	0.20
Bimaxillary width	-0.04	-2.29	1.01	1.07
Palate length	<b>2.94</b>	2.23	<b>2.78</b>	<b>3.66</b>
Bicanine breadth	<b>3.51</b>	1.08	1.40	<b>3.28</b>
Palate breadth	2.24	2.21	-1.66	0.43
Facial height	1.88	2.02	2.16	2.61
Bizygomatic breadth	<b>2.68</b>	-0.21	2.55	<b>3.21</b>
Neurocranial length	-0.06	-1.45	-0.16	0.11
Neurocranial breadth	1.55	1.71	2.57	2.24
Maximum cranial length	1.79	1.08	<b>2.72</b>	2.76
Bimastoid width	-1.67	-2.29	-1.39	-1.15
Postorbital constriction	0.40	-0.37	2.02	0.60
Basicranial length	<b>4.05</b>	<b>2.72</b>	<b>4.78</b>	<b>4.94</b>
Basicranial flexion	<b>3.62</b>	<b>2.73</b>	<b>4.13</b>	<b>4.65</b>
Neurocranial height	-0.30	-2.47	0.96	1.22

**Bold** = significant difference in degree of dimorphism at  $P \leq 0.0125$ .

seven are between two neural variables, similarities which are consistent with the hypotheses of this study. Only three of the statistically significantly similar taxonomic rank orders of degree of dimorphism are between a facial variable and a neural variable. In sum, the Spearman rank-order correlation test demonstrates that a ranking of dimorphic taxa based on body weight does not correlate to a ranking based on facial or neural morphometrics. The choice of a neural or a facial measurement also produces a distinctive taxonomic rank order of dimorphism in the majority of cases.

Indices of adult sexual dimorphism (Table 4) indicate that the crania of the four capuchin species possess moderate to high levels of dimorphism. Specifically, *C. apella* possesses the most sexually dimorphic cranium, whereas *C. olivaceus* possesses the least dimorphic cranium for the measurements included in this study. *Cebus albifrons* and *C. capucinus* possess similar overall levels of dimorphism and fall between *C. apella* and *C. olivaceus*. Greene's (1989) *t*-test (Table 11) indicates that there are no significant interspecific differences in degree of sexual dimorphism in nine of the 15 measurements: biorbital width, facial height, maximum cranial length, neurocranial length, neurocranial breadth, bimastoid breadth, postcanine palate width, basicranial length, and basicranial flexion. Significant interspecific differences are present in the remaining six measurements. In bicanine breadth, *C. apella* and *C. capucinus*

both possess significantly larger degrees of dimorphism than *C. albifrons* and *C. olivaceus*. *Cebus apella* is significantly more dimorphic than *C. capucinus* in postorbital constriction. Significant differences in palate length are present between *C. apella* and *C. olivaceus*. *Cebus apella* is significantly more dimorphic than all other species in bimaxillary breadth, bizygomatic breadth, and neurocranial height.

## DISCUSSION

Interpreting sexual dimorphism depends upon what expression of it is being measured. In attempts to understand cause and effect in dimorphic outcomes the choice of databases alters the degree to which significant dimorphism can be detected (Oxnard, 1983; Leutenegger and Cheverud, 1985; Martin et al., 1994; Ford, 1994; Plavcan and van Schaik, 1997). Recent studies of sexual dimorphism (Plavcan and van Schaik, 1992, 1994, 1997; Ford, 1994) have identified the relative influences of diet, body size, phylogeny, and intraspecific competition on outcomes in body weight and canine size dimorphism. The purpose of this study was to test hypotheses of how dimorphism in New World monkeys is expressed in the cranium and how it is influenced by the effects of localized natural selection, based on predictions of the general phenomenon of dimorphism generated by previous research. The cranial database is used to examine the interaction of dimorphic growth patterns, functional



TABLE 7. *Tg* values for *C. albifrons* vs. nine other New World monkeys

Variables	<i>C. albifrons</i> vs. <i>A. palliata</i>	<i>C. albifrons</i> vs. <i>A. nancymai</i>	<i>C. albifrons</i> vs. <i>A. paniscus</i>	<i>C. albifrons</i> vs. <i>C. calvus</i>	<i>C. albifrons</i> vs. <i>C. cupreus</i>	<i>C. albifrons</i> vs. <i>L. lagotricha</i>	<i>C. albifrons</i> vs. <i>P. pithecia</i>	<i>C. albifrons</i> vs. <i>S. fuscicollis</i>	<i>C. albifrons</i> vs. <i>S. sciureus</i>
Biorbital width	-0.23	<b>2.949</b>	<b>3.64</b>	0.86	2.61	1.71	2.81	<b>3.58</b>	<b>3.27</b>
Bimaxillary width	0.44	<b>8.55</b>	<b>3.23</b>	2.50	<b>6.87</b>	0.38	<b>5.08</b>	<b>7.03</b>	<b>4.74</b>
Palate length	<b>-2.94</b>	<b>2.83</b>	2.22	1.42	<b>3.64</b>	-0.60	2.15	<b>3.33</b>	2.36
Bicanine breadth	<b>-3.51</b>	<b>7.20</b>	<b>4.28</b>	1.48	<b>6.99</b>	-0.61	<b>3.70</b>	<b>6.94</b>	1.36
Palate breadth	-2.24	<b>3.82</b>	<b>3.34</b>	2.32	<b>3.49</b>	<b>3.43</b>	2.60	<b>3.07</b>	<b>5.77</b>
Facial height	-1.88	<b>3.54</b>	2.73	2.04	1.95	1.06	2.77	<b>3.26</b>	<b>2.88</b>
Bizygomatic breadth	-2.68	<b>7.46</b>	<b>3.08</b>	1.72	<b>6.36</b>	1.83	<b>4.00</b>	<b>6.50</b>	<b>4.11</b>
Neurocranial length	0.66	<b>3.59</b>	2.74	1.54	<b>4.12</b>	2.29	<b>3.12</b>	<b>4.95</b>	<b>4.72</b>
Neurocranial breadth	-1.55	2.28	1.24	0.93	1.75	2.36	2.13	2.60	2.75
Maximum cranial length	-1.79	<b>4.01</b>	<b>3.57</b>	1.45	<b>4.43</b>	0.86	<b>3.03</b>	<b>4.36</b>	<b>3.55</b>
Bimastoid width	1.67	<b>5.42</b>	2.72	2.18	<b>4.75</b>	2.46	<b>3.85</b>	<b>4.18</b>	<b>6.24</b>
Postorbital constriction	-0.40	2.32	-0.41	-0.18	1.26	0.61	2.29	2.31	0.86
Basicranial length	<b>-4.05</b>	<b>4.37</b>	<b>3.14</b>	1.27	<b>5.30</b>	2.40	<b>3.48</b>	<b>5.33</b>	<b>4.81</b>
Basicranial flexion	<b>-3.63</b>	<b>5.38</b>	<b>4.80</b>	1.62	<b>5.71</b>	1.35	<b>3.74</b>	<b>5.64</b>	<b>4.67</b>
Neurocranial height	0.30	2.46	1.22	0.51	2.10	<b>3.06</b>	2.79	2.46	2.07

**Bold** = significant difference in degree of dimorphism at  $P \leq 0.005$ .

TABLE 8. *Tg* values for *C. apella* vs. nine other New World monkeys

Variables	<i>C. apella</i> vs. <i>A. palliata</i>	<i>C. apella</i> vs. <i>A. nancymai</i>	<i>C. apella</i> vs. <i>A. paniscus</i>	<i>C. apella</i> vs. <i>C. calvus</i>	<i>C. apella</i> vs. <i>C. cupreus</i>	<i>C. apella</i> vs. <i>L. lagotricha</i>	<i>C. apella</i> vs. <i>P. pithecia</i>	<i>C. apella</i> vs. <i>S. fuscicollis</i>	<i>C. apella</i> vs. <i>S. sciureus</i>
Biorbital width	0.20	<b>4.41</b>	<b>4.93</b>	1.62	<b>3.95</b>	2.78	<b>4.03</b>	<b>5.25</b>	<b>5.06</b>
Bimaxillary width	2.29	<b>8.10</b>	<b>4.49</b>	<b>3.41</b>	<b>6.75</b>	2.41	<b>5.28</b>	<b>6.63</b>	<b>6.90</b>
Palate length	-2.23	<b>6.70</b>	<b>5.18</b>	<b>3.78</b>	<b>7.62</b>	1.55	<b>4.84</b>	<b>7.36</b>	<b>6.86</b>
Bicanine breadth	-1.09	<b>9.60</b>	<b>6.48</b>	<b>3.36</b>	<b>9.13</b>	2.13	<b>5.46</b>	<b>8.89</b>	<b>4.94</b>
Palate breadth	-2.22	<b>5.56</b>	<b>4.65</b>	<b>3.46</b>	<b>5.12</b>	<b>5.06</b>	<b>3.71</b>	<b>4.56</b>	<b>8.25</b>
Facial height	-2.02	<b>4.04</b>	<b>3.14</b>	2.34	2.27	1.30	<b>3.15</b>	<b>3.71</b>	<b>3.35</b>
Bizygomatic breadth	0.21	<b>9.37</b>	<b>5.32</b>	<b>3.64</b>	<b>8.17</b>	<b>4.91</b>	<b>5.63</b>	<b>8.12</b>	<b>7.80</b>
Neurocranial length	1.46	<b>4.41</b>	<b>3.51</b>	2.17	<b>4.74</b>	<b>3.32</b>	<b>3.60</b>	<b>5.42</b>	<b>5.95</b>
Neurocranial breadth	-1.72	<b>3.00</b>	1.66	1.27	2.34	<b>3.03</b>	2.71	<b>3.38</b>	<b>3.57</b>
Maximum cranial length	-1.08	<b>6.70</b>	<b>5.82</b>	<b>2.94</b>	<b>7.10</b>	2.61	<b>4.81</b>	<b>7.03</b>	<b>6.47</b>
Bimastoid width	2.30	<b>6.25</b>	<b>3.42</b>	2.74	<b>5.52</b>	<b>3.33</b>	<b>4.43</b>	<b>4.87</b>	<b>7.47</b>
Postorbital constriction	0.37	<b>3.84</b>	0.29	0.50	2.44	1.73	<b>3.63</b>	<b>3.90</b>	2.24
Basicranial length	-2.72	<b>5.72</b>	<b>4.33</b>	2.28	<b>6.43</b>	<b>3.96</b>	<b>4.40</b>	<b>6.33</b>	<b>6.74</b>
Basicranial flexion	-2.73	<b>7.03</b>	<b>6.23</b>	2.67	<b>7.24</b>	<b>2.82</b>	<b>4.87</b>	<b>7.09</b>	<b>6.81</b>
Neurocranial height	2.48	<b>4.85</b>	2.63	2.28	<b>4.45</b>	<b>5.34</b>	<b>4.58</b>	<b>4.77</b>	<b>5.26</b>

**Bold** = significant difference in degree of dimorphism at  $P \leq 0.005$ .

TABLE 9. *Tg* values for *C. capucinus* vs. nine other New World monkeys

Variables	<i>C. capucinus</i> vs. <i>A. palliata</i>	<i>C. capucinus</i> vs. <i>A. nancymai</i>	<i>C. capucinus</i> vs. <i>A. paniscus</i>	<i>C. capucinus</i> vs. <i>C. calvus</i>	<i>C. capucinus</i> vs. <i>C. cupreus</i>	<i>C. capucinus</i> vs. <i>L. lagotricha</i>	<i>C. capucinus</i> vs. <i>P. pithecia</i>	<i>C. capucinus</i> vs. <i>S. fuscicollis</i>	<i>C. capucinus</i> vs. <i>S. sciureus</i>
Biorbital width	-0.77	2.68	<b>3.49</b>	0.46	2.36	1.18	2.76	<b>3.63</b>	2.74
Bimaxillary width	-1.02	<b>5.03</b>	1.54	0.67	<b>3.78</b>	-0.91	<b>3.03</b>	<b>3.92</b>	1.95
Palate length	-2.79	<b>5.09</b>	<b>3.84</b>	2.73	<b>6.04</b>	0.41	<b>3.72</b>	<b>5.88</b>	<b>4.82</b>
Bicanine breadth	-1.40	<b>10.87</b>	<b>6.95</b>	<b>3.58</b>	<b>10.50</b>	1.96	<b>5.76</b>	<b>10.44</b>	<b>4.89</b>
Palate breadth	1.67	<b>11.08</b>	<b>8.00</b>	<b>7.19</b>	<b>10.31</b>	<b>10.44</b>	<b>7.10</b>	<b>9.53</b>	<b>15.66</b>
Facial height	-2.17	<b>4.45</b>	<b>3.32</b>	2.63	2.55	1.32	<b>3.45</b>	<b>4.39</b>	<b>3.55</b>
Bizygomatic breadth	-2.56	<b>9.06</b>	<b>3.75</b>	2.22	<b>7.79</b>	2.43	<b>4.70</b>	<b>7.85</b>	<b>5.00</b>
Neurocranial length	0.16	<b>2.89</b>	2.20	1.01	<b>3.42</b>	1.63	2.58	<b>4.28</b>	<b>3.84</b>
Neurocranial breadth	-2.57	1.74	0.69	0.46	1.19	1.79	1.84	2.27	1.97
Maximum cranial length	-2.73	<b>5.63</b>	<b>4.77</b>	1.86	<b>6.31</b>	0.74	<b>3.93</b>	<b>6.59</b>	<b>4.32</b>
Bimastoid width	1.14	<b>5.33</b>	2.46	1.97	<b>4.65</b>	2.08	<b>3.78</b>	<b>4.08</b>	<b>5.94</b>
Postorbital constriction	-2.02	1.40	-1.72	-1.41	0.23	-0.73	1.79	1.56	-0.77
Basicranial length	<b>-4.79</b>	<b>5.48</b>	<b>3.79</b>	1.76	<b>7.02</b>	<b>3.05</b>	<b>4.40</b>	<b>7.26</b>	<b>5.99</b>
Basicranial flexion	<b>-4.13</b>	<b>7.71</b>	<b>6.55</b>	2.47	<b>8.26</b>	2.06	<b>4.93</b>	<b>8.65</b>	<b>6.53</b>
Neurocranial height	-0.96	1.14	0.54	-0.50	0.73	1.92	1.71	1.01	0.34

**Bold** = significant difference in degree of dimorphism at  $P \leq 0.005$ .

TABLE 10. *Tg* values for *C. olivaceus* vs. nine other New World monkeys

Variables	<i>C. olivaceus</i> vs. <i>A. palliata</i>	<i>C. olivaceus</i> vs. <i>A. nancymai</i>	<i>C. olivaceus</i> vs. <i>A. paniscus</i>	<i>C. olivaceus</i> vs. <i>C. calvus</i>	<i>C. olivaceus</i> vs. <i>C. cupreus</i>	<i>C. olivaceus</i> vs. <i>L. lagotricha</i>	<i>C. olivaceus</i> vs. <i>P. pithecia</i>	<i>C. olivaceus</i> vs. <i>S. fuscicollis</i>	<i>C. olivaceus</i> vs. <i>S. sciureus</i>
Biorbital width	-0.20	<b>3.04</b>	<b>3.64</b>	0.91	2.69	1.75	<b>2.89</b>	<b>3.72</b>	<b>3.37</b>
Bimaxillary width	-1.07	<b>4.47</b>	1.30	0.50	<b>3.32</b>	-0.97	2.69	<b>3.46</b>	1.60
Palate length	<b>-3.66</b>	<b>3.29</b>	2.47	1.58	<b>4.32</b>	-0.91	2.48	<b>4.12</b>	2.55
Bicanine breadth	<b>-3.29</b>	<b>6.96</b>	<b>4.15</b>	1.46	<b>6.76</b>	-0.52	<b>3.58</b>	<b>6.72</b>	1.39
Palate breadth	-0.44	<b>7.07</b>	<b>5.44</b>	<b>4.50</b>	<b>6.53</b>	<b>6.58</b>	<b>4.63</b>	<b>5.95</b>	<b>10.21</b>
Facial height	-2.61	<b>3.53</b>	2.61	1.99	1.72	0.54	2.80	<b>3.45</b>	2.45
Bizygomatic breadth	<b>-3.21</b>	<b>7.35</b>	2.74	1.42	<b>6.24</b>	1.35	<b>3.78</b>	<b>6.40</b>	<b>3.53</b>
Neurocranial length	-0.01	2.30	1.78	0.70	2.71	1.25	2.06	<b>3.45</b>	<b>3.14</b>
Neurocranial breadth	-2.24	1.58	0.65	0.44	1.10	1.67	1.68	2.03	1.84
Maximum cranial length	-2.77	<b>4.51</b>	<b>3.92</b>	1.34	<b>5.14</b>	0.30	<b>3.28</b>	<b>5.27</b>	<b>3.39</b>
Bimastoid width	1.16	<b>4.79</b>	2.10	1.69	<b>4.18</b>	1.74	<b>3.41</b>	<b>3.62</b>	<b>5.35</b>
Postorbital constriction	-0.60	2.43	-0.56	-0.32	1.27	0.53	2.52	2.56	0.75
Basicranial length	<b>-4.95</b>	<b>4.22</b>	<b>2.92</b>	1.00	<b>5.45</b>	2.00	<b>3.44</b>	<b>5.59</b>	<b>4.46</b>
Basicranial flexion	<b>-4.66</b>	<b>5.17</b>	<b>4.58</b>	1.20	<b>5.66</b>	0.63	<b>3.52</b>	<b>5.75</b>	<b>3.95</b>
Neurocranial height	-1.23	0.94	0.42	-0.70	0.52	1.73	1.58	0.81	0.04

**Bold** = significant difference in degree of dimorphism at  $P \leq 0.005$ .

TABLE 11. *Tg* values for *Cebus* interspecific comparisons

Variables	<i>C. apella</i> vs. <i>C. albifrons</i>	<i>C. apella</i> vs. <i>C. capucinus</i>	<i>C. apella</i> vs. <i>C. olivaceus</i>	<i>C. capucinus</i> vs. <i>C. albifrons</i>	<i>C. capucinus</i> vs. <i>C. olivaceus</i>	<i>C. olivaceus</i> vs. <i>C. albifrons</i>
Biorbital width	0.66	1.57	0.61	-0.68	-0.73	0.04
Bimaxillary width	<b>2.98</b>	<b>4.43</b>	<b>4.28</b>	-2.15	0.18	-2.20
Palate length	2.20	1.23	<b>2.80</b>	1.04	1.47	-0.21
Bicanine breadth	<b>3.06</b>	0.25	<b>2.83</b>	<b>2.92</b>	<b>2.70</b>	0.08
Palate breadth	0.70	0.27	1.93	0.88	2.18	-0.93
Facial height	0.11	0.05	0.79	0.06	0.78	-0.60
Bizygomatic breadth	<b>3.42</b>	<b>3.13</b>	<b>3.87</b>	0.49	1.08	-0.54
Neurocranial length	1.19	1.85	1.92	-0.70	0.23	-0.85
Neurocranial breadth	0.20	1.22	1.06	-0.83	-0.05	-0.72
Maximum cranial length	1.42	2.17	2.43	-0.34	0.44	-0.65
Bimastoid width	0.76	1.35	1.57	-0.53	0.27	-0.76
Postorbital constriction	0.99	<b>3.01</b>	1.24	-1.46	-1.47	-0.13
Basiscranial length	1.60	1.56	2.21	0.20	0.89	-0.57
Basiscranial flexion	1.44	1.12	2.38	0.48	1.54	-0.83
Neurocranial height	<b>2.82</b>	<b>4.36</b>	<b>4.67</b>	-1.55	0.27	-1.85

**Bold** = significant difference in degree of dimorphism at  $P \leq 0.008$ .

TABLE 12. Spearman rank-order coefficients for comparisons of taxonomic rank orders by facial and neural measurements in the nine genera dimorphic for body weight

	Wt	BCB (F)	BMB (F)	BZB (F)	PAB (F)	PAL (F)	BOB (N)	BMW (N)	NCB (N)	NCH (N)	NCL (N)	POC (N)
Wt	1.000											
BCB	0.521	1.000										
BMB	0.363	0.662	1.000									
BZB	0.775	0.866*	0.767	1.000								
PAB	0.802	0.713	0.711	0.830*	1.000							
PAL	0.477	0.871*	0.865*	0.809	0.805	1.000						
BOB	0.764	0.485	0.562	0.813	0.708	0.483	1.000					
BMW	0.824	0.513	0.607	0.814	0.785	0.612	0.928*	1.000				
NCB	0.729	0.681	0.807	0.893*	0.906*	0.723	0.838*	0.809	1.000			
NCH	0.627	0.515	0.723	0.814	0.660	0.504	0.793	0.708	0.857*	1.000		
NCL	0.809	0.528	0.691	0.850*	0.821	0.624	0.957*	0.979*	0.893*	0.817	1.000	
POC	0.461	0.549	0.594	0.704	0.582	0.472	0.670	0.549	0.717	0.888*	0.658	1.000

Facial (F) and neural (N) measurements are indicated, and significantly similar taxonomic rank orders for degree of dimorphism at  $P < 0.01$  are denoted by an asterisk (\*).

morphology, and natural selection, three facets of primate biology subsumed within a general database such as body weight.

In general, we find that the pattern of dimorphism in the cranium follows the pattern of dimorphism in body size to the extent that taxa such as *Alouatta* and *Cebus* are dimorphic for both measures. Within the cranium, variables that account for neural size show greater degrees of dimorphism in *Cebus*, which is one of the only New World monkeys with a relatively large brain (Hartwig, 1996). Variables that account for facial size show greater degrees of dimorphism in taxa for which other selective pressures for larger jaw size are in effect (*Alouatta*, *Cebus apella*).

Taxonomic rank orderings of dimorphism (Table 4) demonstrate that species are not

equivalently dimorphic across the different functional regions of the cranium, and that dimorphism is not expressed in the cranium as a whole or in parts in a manner consistent with rankings of general body size or canine size dimorphism (Tables 3, 12). Taxonomic rank orderings of dimorphism confirm the prediction of the first hypothesis that different regions of the cranium (neurocranium, face, dental arcade) will not display equivalent degrees of dimorphism within the same species, nor produce equivalent relative rank orderings across species. The implication of Table 4 is that degree of dimorphism in the cranium is driven by both growth constraints associated with different functional regions and by the independent action of natural selection on the morphology of those regions.

A measure of significance is needed to place these rank orderings in the proper context and to identify which parts of the cranium display the greatest degrees of difference in sexual dimorphism across taxa. Greene's (1989) *t*-test is a relatively simple measure of how much more dimorphic one species is compared to another. This statistic indicates not only that *Alouatta* and *Cebus* are dimorphic, but that they are significantly more dimorphic than most other New World monkeys for the majority of variables measured in this study. The test also indicates that although dimorphism in *Cebus apella* outranks dimorphism in *Alouatta* for several neurocranial measurements (and vice-versa for facial, basicranial, and dental measurements), in no case is the difference between them statistically significant. By contrast, the degree of dimorphism in *Alouatta* is significantly greater than the degree of dimorphism in all other taxa for measures of basicranial length and flexion.

We investigated *Cebus* in more detail because all species show pronounced dimorphism, but one of them, *C. apella*, is more specialized in its feeding habits (Terborgh 1983, Janson 1985, Janson and Boinski 1992). Although *C. capucinus* possesses the largest index of body weight dimorphism (Ford and Davis, 1992), it does not exhibit the largest degree of canine and cranial dimorphism. Data on reproductive behavior suggest that *C. apella* and *C. olivaceus* are subjected to a stronger degree of sexual selection than *C. albifrons* and *C. capucinus* because only one male tends to do the majority of mating in the former two species (Janson, 1984, 1986a,b; Robinson 1988a,b; Fedigan, 1993). This suggests that *C. apella* and *C. olivaceus* should possess a larger degree of canine and cranial dimorphism than both *C. albifrons* and *C. capucinus* if intermale competition is the primary underlying causal factor. The lack of canine data for *C. albifrons* and *C. olivaceus* precludes us from examining the relationship between male-male competition and canine dimorphism in detail; however, the data that are available suggest that *C. apella* possesses a larger index of canine dimorphism than *C. capucinus*, as expected given their known reproductive behavior.

Within the cranium, our results corroborate that *C. apella* is the most dimorphic species of the genus, especially in somatic (facial) measurements. Surprisingly, *C. olivaceus* is the least dimorphic species, a finding that is contrary to what is expected given the behavioral data of this species. *Cebus olivaceus* does possess the lowest index of body weight dimorphism (Ford and Davis, 1992), which may help explain the relatively small degree of cranial dimorphism. It may also be that there is a strong presence of female-female competition for resources that is increasing female size in *C. olivaceus*. This finding merits further study. The high level of sexual dimorphism in *C. apella* may be related to differences in foraging behavior, diet, and mandibular size/shape relationships among the capuchins. In each case, *C. apella* is substantially different from the other capuchins (see Masterson, 1996, 1997). For example, *C. apella* is significantly more dimorphic than the other three species in three measurements related to the masticatory apparatus: bimaxillary breadth, bizygomatic breadth, and neurocranial height. Specifically, male tufted capuchins possess significantly larger infratemporal fossae and therefore larger muscles of mastication than female tufted capuchins. While moderate to high levels of sexual dimorphism do exist in the other capuchins in these same measurements, *C. apella* is clearly different. These differences correspond to the slightly different ecological niche of *C. apella* compared to other *Cebus* species (Masterson, 1996).

## CONCLUSIONS

The degree of sexual dimorphism expressed in the cranium of New World monkeys is influenced by several factors, including the effects of natural selection on specific regions of the cranium. Capuchin and howler monkeys are dimorphic for both body size and canine size. They differ, however, in that *Cebus* is typically more dimorphic than other taxa for neural measurements and *Alouatta* is typically more dimorphic than other taxa for somatic (facial) measurements. Spearman rank-order correlation tests for degree of dimorphism show that within-domain rank orders (i.e., neural vs. neural vari-

ables) are more frequently similar to one another than are between-domain rank orders (i.e., neural vs. facial variables). The capuchin monkey pattern may be due to the compounding effects of selection for relative brain size increase. The howler monkey pattern may be due to its enlarged hyoid and the effect this derivation has on the relative size and displacement of the face (Rosenberger and Strier, 1989). Phylogeny and overall body size, as measured by body mass, have no obvious influence on the degree and pattern of cranial dimorphism in New World monkeys, which agrees with previous work on body size dimorphism (Ford, 1994; Plavcan and van Schaik, 1997).

Within *Cebus*, *C. apella* is consistently significantly more dimorphic than other *Cebus* species for somatic (facial) measurements, but not for neural or body weight measurements. While high overall dimorphism in *Cebus* is probably driven by male-male competition (Ford, 1994), the pattern in *C. apella* suggests that the degree of dimorphism is enhanced by other selective pressures such as dietary adaptation (Masterson, 1996, 1997). In general, we find that the pattern of dimorphism in New World monkeys as reflected by Greene's (1989) *t*-test is a mosaic condition influenced more by anatomical adaptations particular to the species in question than by general factors such as body size or phylogeny.

#### ACKNOWLEDGMENTS

We thank Marian Dagosto and Brian Shea for use of the Reflex microscope. For access to specimens under their care, we thank Richard W. Thorington of the NMNH, Bruce Patterson of the FMNH, and RDE MacPhee, Guy Musser, and Wolfgang Fuchs of the AMNH. We thank Emöke Szathmáry and an anonymous reviewer for their effort to improve the manuscript. This research was supported in part by a grant from Sigma XI (TJM), and a University of California Regents Fellowship (WCH).

#### LITERATURE CITED

- Albrecht GH, Gelvin BR, and Hartman SE (1993) Ratios as a size-adjustment in morphometrics. *Am. J. Phys. Anthropol.* 91:441–468.
- Cheverud J, Dow M, and Leutenegger W (1985) The quantitative assessment of phylogenetic constraints in comparative analysis: Sexual dimorphism in body weight among primates. *Evolution* 39:1335–1351.
- Clutton-Brock TH (1985) Size, sexual dimorphism, and polygyny in primates. In WL Jungers (ed.): *Size and Scaling in Primate Biology*. New York: Plenum Press, pp. 51–60.
- Clutton-Brock TH, Harvey PH, and Rudder B (1977) Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature* 269:191–195.
- Fedigan LM (1993) Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *Int. J. Primatol.* 14:853–877.
- Ford SM (1994) Evolution of sexual dimorphism in body weight in platyrrhines. *Am. J. Primatol.* 34:221–244.
- Ford SM, and Davis LC (1992) Systematics and body size: Implications for feeding adaptations in New World monkeys. *Am. J. Phys. Anthropol.* 88:415–468.
- Gaulin S, and Sailer L (1984) Sexual dimorphism in weight among primates: The relative impact of allometry and sexual selection. *Int. J. Primatol.* 5:515–535.
- Greene DL (1989) Comparison of *t*-tests for differences in sexual dimorphism between populations. *Am. J. Phys. Anthropol.* 79:121–125.
- Greenfield LO (1992) Relative canine size, behavior and diet in male cebids. *J. Hum. Evol.* 23:469–480.
- Hartwig WC (1993) Comparative Morphology, Ontogeny and Phylogenetic Analysis of the Platyrrhine Cranium. Ph.D. thesis, University of California at Berkeley.
- Hartwig WC (1996) Perinatal life history traits in New World monkeys. *Am. J. Primatol.* 40:99–130.
- Harvey P, Martin RD, and Clutton-Brock TH (1987) Life histories in comparative perspective. In BB Smuts, DL Cheney, RM Seyfarth, and RW Wrangham (eds.): *Primate Societies*. Chicago: University of Chicago Press, pp. 181–196.
- Janson CH (1984) Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). *Z. Tierpsychol.* 65:177–200.
- Janson CH (1985) Aggressive competition and individual food intake in wild brown capuchin monkeys. *Behav. Ecol. Sociobiol.* 18:125–138.
- Janson CH (1986a) Capuchin counterpoint. *Natural History* 95:45–53.
- Janson CH (1986b) The mating system as a determinant of social evolution in capuchin monkeys. In J Else and PC Lee (eds.): *Primate Ecology and Conservation*. Cambridge: Cambridge University Press, pp. 169–179.
- Janson CH, and Boinski S (1992) Morphological and behavioral adaptations for foraging in generalist primates: The case of the cebines. *Am. J. Phys. Anthropol.* 88:483–498.
- Jungers WL, Falsetti AB, and Wall CE (1995) Shape, relative size, and size-adjustments in morphometrics. *Am. J. Phys. Anthropol. Supp* 38:137–161.
- Kappeler PM (1990) The evolution of sexual size dimorphism in prosimian primates. *Am. J. Primatol.* 21:201–214.
- Kappeler PM (1991) Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatol.* 57:132–146.
- Kay RF, Plavcan JM, Glander KE, and Wright PC (1988) Sexual selection and canine dimorphism in New World monkeys. *Am. J. Phys. Anthropol.* 77:385–397.
- Kinzey WG (1974) Ceboid models for the evolution of hominoid dentition. *J. Hum. Evol.* 3:193–203.
- Konigsberg LW (1991) An historical note on the *t*-test for differences in sexual dimorphism between populations. *Am. J. Phys. Anthropol.* 84:93–97.
- Leigh SR (1992) Patterns of variation in the ontogeny of primate body size dimorphism. *J. Hum. Evol.* 23:27–50.



- Leigh SR (1994) Relations between captive and noncaptive weights in anthropoid primates. *Zoo Biol.* 13: 21–43.
- Leigh SR (1995) Socioecology and the ontogeny of sexual size dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* 97:339–356.
- Leutenegger W (1978) Scaling of sexual dimorphism in body size and breeding system in primates. *Nature* 272:610–611.
- Leutenegger W, and Cheverud JM (1982) Correlates of sexual dimorphism in primates: Ecological and size variables. *Int. J. Primatol.* 3:387–402.
- Leutenegger W, and Cheverud JM (1985) Sexual dimorphism in primates: The effects of size. In WL Jungers (ed.): *Size and Scaling in Primate Biology*. New York: Plenum Press, pp.33–50.
- Leutenegger W, and Kelly JT (1977) Relationship of sexual dimorphism in canine size and body size to social, behavioral and ecological correlates in anthropoid primates. *Primates* 18:117–136.
- Martin RD, Willner LA, and Dettling A (1994) The evolution of sexual size dimorphism in primates. In RV Short and E Balaban (eds.): *The Differences Between the Sexes*. Cambridge: Cambridge University Press, pp. 159–200.
- Masterston TJ (1996) Cranial Form in *Cebus*: An Ontogenetic Analysis of Cranial Form and Sexual Dimorphism. Ph.D. thesis, University of Wisconsin-Madison.
- Masterston TJ (1997) Sexual dimorphism and interspecific cranial form in two capuchin species: *Cebus albifrons* and *C. apella*. *Am. J. Phys. Anthropol.* 104:487–512.
- Oxnard CD (1983) Sexual dimorphism in the overall proportions of primates. *Am. J. Primatol.* 4:1–22.
- Oxnard CD, Lieberman SS, and Gelvin BR (1985) Sexual dimorphisms in dental dimensions of higher primates. *Am. J. Primatol.* 8:127–152.
- Pickford M (1986) On the origins of body size dimorphism in primates. In M Pickford and B Chiarelli (eds.): *Sexual Dimorphism in Living and Fossil Primates*. Firenze: Il Sedicesimo, pp. 77–91.
- Plavcan JM, and Kay RF (1988) Sexual dimorphism and dental variability in platyrrhine primates. *Int. J. Primatol.* 9:169–178.
- Plavcan JM, and van Schaik CP (1992) Intrasexual competition and canine dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* 87:461–477.
- Plavcan JM, and van Schaik CP (1994) Canine dimorphism. *Evol. Anthropol.* 2:208–214.
- Plavcan JM, and van Schaik CP (1997) Intrasexual competition and body weight dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* 103:37–68.
- Relethford JH, and Hodges DC (1985) A statistical test for differences in sexual dimorphism between populations. *Am. J. Phys. Anthropol.* 66:55–61.
- Robinson JG (1988a) Demography and group structure in wedge-capped capuchin monkeys, *Cebus olivaceus*. *Behaviour* 104:202–232.
- Robinson JG (1988b) Group size in wedge-capped capuchin monkeys (*Cebus olivaceus*) and the reproductive success of males and females. *Behav. Ecol. Sociobiol.* 23:187–197.
- Rosenberger AL, and Strier AL (1989) Adaptive radiation of the ateline primates. *J. Hum. Evol.* 18:717–750.
- Schneider H, and Rosenberger AL (1996) Molecules, morphology, and platyrrhine systematics. In MA Norconk, AL Rosenberger, and PA Garber (eds.): *Adaptive Radiations of Neotropical Primates*. New York: Plenum Press, pp. 3–20.
- Smith RJ (1996) Sexual dimorphism in *Ateles paniscus* body mass. *J. Hum. Evol.* 31:69–73.
- Smith RJ, and Jungers WL (1997) Body mass in comparative primatology. *J. Hum. Evol.* 32:523–559.
- Sokal RR, and Rohlf FJ (1995) *Biometry*, 3rd ed. New York: WH Freeman.
- Terborgh JW (1983) *Five New World Primates*. Princeton, N.J.: Princeton University Press.
- Zar JH (1984) *Biostatistical Analysis*, 2nd ed. Englewood Cliffs, N.J.: Prentice-Hall.